PHRAGMOCONE IMPLOSION IN ORDOVICIAN NAUTILOIDS AND THE FUNCTION OF SIPHONAL DIAPHRAGMS AND ENDOCONES

by DAVID H. EVANS

ABSTRACT. Two species of nautiloid – a new genus and species of Cyclostomiceratidae and a new species of *Dideroceras* from the Llanvirn Series of Wales and western Shropshire – show preservational features which suggest that the adapical portions of the phragmocones imploded after the death of the organism. The limit of phragmocone damage is close to the most adoral development of siphonal diaphragms or endocones. It is thought that the apical part of the phragmocone was partly or completely filled with gas, failing to flood or flooding very slowly after the death of the organism. Either increased hydrostatic pressure or a decrease in shell strength, or a combination of both factors, brought about phragmocone failure. The function of siphonal diaphragms, and in part that of endocones, is interpreted as reducing the metabolic cost of pumping liquid away from camerae which would otherwise become flooded, and would consequently disturb the organism's hydrostatic equilibrium.

RECENT studies on cephalopod taphonomy have attempted to assess the significance of septal and siphuncular damage as a result of cameral implosion and their potential use in bathymetric studies (Westermann 1973, 1975, 1985; Hewitt and Westermann 1987, 1988*a*, 1988*b*; Hewitt 1988; Stridsberg 1990). These studies, when using fossil material, have relied on the presence of well-preserved septa or septal fragments to estimate the strength of the septa and thus the depth at which they failed under hydrostatic pressure. In this paper, another aspect of phragmocone damage thought to be brought about by implosion of the phragmocone wall is explored.

A cyclostomiceratid and *Dideroceras* sp. nov. (Evans in prep.) occur together in molluscan-dominated faunas of Llanvirn Series age in Wales and western Shropshire. No estimate of septal strength can be given for either species because specimens are either internal moulds or have septa preserved in too recrystallized a state to attempt reasonable estimates of thickness and thus of strength. These phragmocones appear to show no evidence of septal implosion, but instead are often preserved with the apical part of the phragmocone truncated. No apical portions of phragmocones have been recovered. Significantly, in sufficiently well-preserved specimens it can be seen that truncation took place at or close to the most adoral development of siphonal diaphragms or endocones. It is argued below that this mode of preservation resulted from failure of the camerae of the apical portion of the phragmocone to reach equilibrium with the ambient hydrostatic pressure after death. Disequilibrium resulted in the apical portion of the phragmocone imploding either during sinking into deep water (as suggested by Raup 1973) or after a prolonged period during which degradation of the organic components of the shell took place. Whichever process caused it, implosion provides a clue to the possible function of siphonal diaphragms; a partial explanation for that of endocones may also be possible.

MATERIAL

All the material described or discussed below is deposited in the National Museum of Wales (NMW 88.30G.54–66, 202–206).

Localities and horizons. The two species were found together at two different locations of Llanvirn Series age (Text-fig. 1):

1. Weston Member, Middleton Formation, upper Llanvirn Series, *Didymograptus murchisoni* Biozone, Priestweston Quarry, Shropshire (National Grid Reference SO 2952 9730).

2. Siltstone lenticle from the lower Llanvirn Series *Didymograptus artus* Biozone in the Camnant Brook (section **a** of Elles 1940, p. 393), Powys (N.G.R. SO 0884 5730).

TEXT-FIG. 1. Map of part of England and Wales showing distribution of Ordovician outcrop and the sites of the localities described in the text.
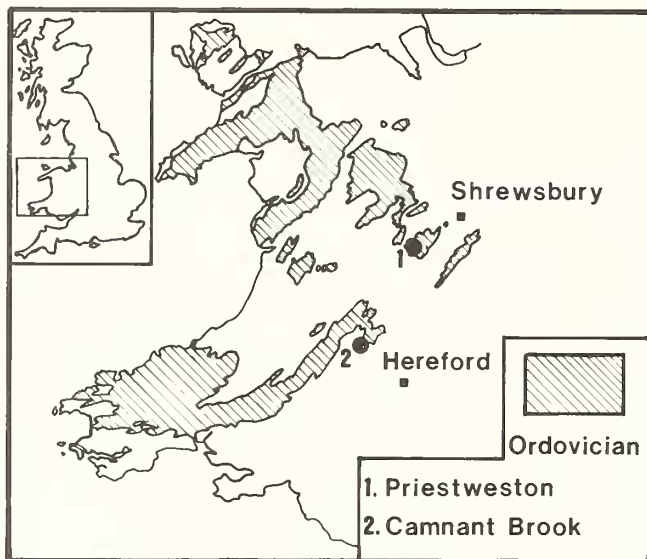

Sediments and fauna. Priestweston Quarry: the Weston Member at Priestweston Quarry consists of siltstones with occasional coarse sandstones (Text-fig. 2). The siltstones, which may be parted by thin developments of shale, are occasionally ripple laminated, and hummocky cross-stratification may also be developed in places. Bioturbation is common in some horizons. Fossils are not common and tend to occur in pockets. In addition to the cephalopods, the fauna consists of brachiopods including *Palaeoglossa attenuata* (J. de C. Sowerby), *Pseudolingula spatula* Williams and *Tissintia prototypa* (Williams). Bellerophontids also occur and infaunal bivalves are present but rare. Trilobites include *Ogyginus corndensis* (Murchison), and *Platycoryphe vulcani* (Murchison) was recorded as the typical species of the Weston Member (Whittard 1979, table 4). Bryozoans are rare.

Camnant Brook: The succession at this location was described by Elles (1940, p. 393). It consists of siltstones and fine sandstones (Text-fig. 2). The latter are lenticular. Ripple lamination, hummocky cross-stratification and bioturbation are all evident. The fine sandstones are normally thin (0·05–0·3 m), and commonly contain coquinas. In the siltstones, fossils are more sporadic. The fauna of the fine sandstones is dominated by infaunal and semi-faunal bivalves (Dr J. C. W. Cope, pers. comm. 1988), the majority of which are disarticulated. Brachiopods are represented by *Pseudolingula* and *Tissintia* (Lockley and Williams 1981). Specimens of both are disarticulated, and are often broken and comminuted. Bellerophontids and gastropods are fairly common. Trilobites are represented by *Ogyginus corndensis*, *Platycoryphe vulcani* and *Plaesiacomia* sp. Bryozoans are rare and extremely fragmentary.

Discussion. The faunas of the two localities, although of slightly differing age, are qualitatively similar in composition. In both, the brachiopod fauna falls within the *Tissintia prototypa*

Priestweston

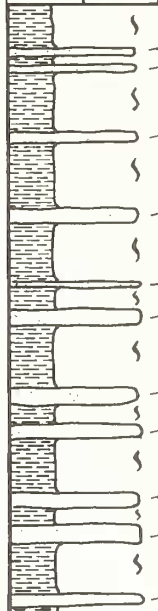| Silt-stn.	f. sst.	m. sst.	c. sst.
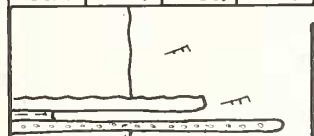
Camnant

Silt-stn.	f. sst.

Key:

- ⌒ Ripple lamination
- ≋ Hummoc-ky X strat.
- �ↄ Coquina
- ∫ Bioturb-ated
- ☆ Cephalo-pod hori-zon.

palaeocommunity of Williams *et al.* (1981, p. 680). The difference between the fauna of Priestweston Quarry and that of the Camnant Brook lies in the concentration, disarticulation and breakage of shells in the latter. This is taken to indicate that the fossils of the fine sandstones of the Camnant Brook section have been transported. Despite the sporadic occurrence of fossils at Priestweston Quarry, there is very little evidence of shell breakage except of the cephalopods; bivalves, although rare, are articulated. It seems likely that the fauna from Priestweston Quarry underwent very little transport.

Collection of material. Material from Camnant Brook was collected in bulk from a single lenticle and extracted using a hydraulic rock splitter. The sporadic occurrence of fossils at Priestweston Quarry necessitated several visits to the site.
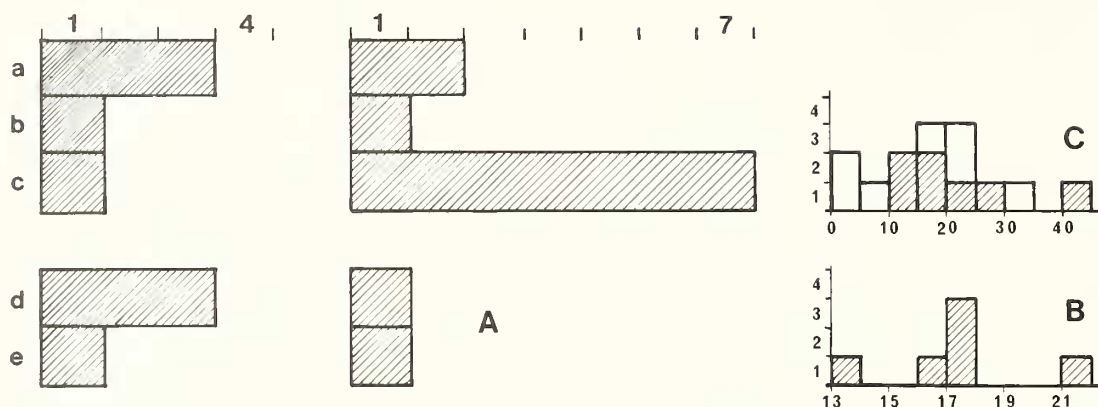
PRESERVATION OF THE CEPHALOPODS

Cyclostomiceratid. Preservation typically consists of adoral portions of phragmocone and body-chamber, while the adapical portion of the phragmocone is missing (Text-fig. 3). Siphuncles are invested with sediment. Some camerae contain sparite.

In NMW 88.30G.202 the adapical portion of the preserved portion of the siphuncle contains diaphragms; sparite is present between them. When diaphragms have been fractured or broken (Text-fig. 4B), sediment is present in the spaces between them. Camerae adapical to the development of the diaphragms have septa that are either badly damaged or missing but, where present, the camerae are infilled with sediment. Body-chambers usually show some sign of having been compressed during burial. Where the phragmocones contained sediment, compression also occurred to varying degrees.

Dideroceras. A number of specimens are known only from the external mould of the endocone-

TEXT-FIG. 3. Histographs detailing preservational characteristics of cephalopods recovered from Priestweston Quarry and Camnant Brook. A, parts of conch preserved. *a–c, Dideroceras* sp. nov.; *a*, phragmocones with empty siphuncles; *b*, phragmocones with siphuncles containing endocones; *c*, loose endosiphuncles. *d–e*, Cyclostomiceratidae gen. et sp. nov.; *d*, truncated phragmocones with body-chambers attached; *e*, phragmocones only. B, Cyclostomiceratidae gen. et sp. nov.; diameter of phragmocone at position of truncation (mm). C, *Dideroceras* sp. nov. mean diameters of preserved portions of phragmocones (mm). Unfilled blocks represent loose endosiphuncles which have been included by doubling their diameters giving their approximate phragmocone diameters.

bearing portion of the siphuncle. Otherwise, preservation is similar to that described for the cyclostomiceratid. It differs in that in some cases the ectosiphuncle and endocones may still protrude from the otherwise truncated phragmocone (Text-fig. 3). Damage to the phragmocone occurs just adapically to the most adoral development of the endocones (Text-fig. 4E).

Comparison of preservation at the sites. Although the number of specimens involved is small and uncertainties exist through the lack of systematic sampling, several differences in preservation between the two localities are observed (Text-fig. 3):

1. Difference in the overall proportions of taxa present: the cyclostomiceratid accounts for four out of nine specimens collected from Priestweston, but only two out of eleven specimens from Camnant Brook.

2. The degree of penetration of sediment into camerae differs. At Camnant Brook, sediment penetrated camerae in every case where the phragmocone is preserved. At Priestweston, phragmocones are commonly crushed (indicating that little sediment penetrated the camerae), but, if undeformed, consist either of a sparite-filled phragmocone or an external mould after a sparite-filled phragmocone.

3. At Camnant Brook, six out of nine specimens of *Dideroceras* are represented by loose and broken endosiphuncles, compared with one out of the five specimens from Priestweston Quarry.

Examples of similar modes of preservation elsewhere. Other than at the localities under study, the adapical truncation of phragmocones close to the adoral development of diaphragms or endocones is either unusual or difficult to recognize. Nevertheless, at least one identical example of this type of preservation is known: *Pictetoceras eichwaldi* (Verneuil) from the Kunda Stage (B_{III_γ}) of Estonia (Mutvei and Stumbur 1971, pl. 1, figs 1–3; Text-fig. 4A). In this case, the adoral camerae (except where the connecting ring is broken) are infilled with sparite. Adapical camerae are filled with sediment only or are missing. Diaphragms when undamaged have sparite between them, but when fractured sediment is present (Mutvei and Stumbur 1971, pl. 3, fig. 2).

Since many ellesmerocerids possessed diaphragms, it might be expected that similar modes of damage would also be found amongst them. This is very difficult to demonstrate. A number of examples of ellesmerocerids and piloceratids showing siphuncles preserved for some distance beyond truncated phragmocones may represent this type of preservation (Text-fig. 4D–F). Occasionally, thin and opaque sections may also demonstrate this mode of preservation (for example *Leviscoceras*? sp., Ulrich *et al.* 1943, pl. 62, figs 14–15; *Ecteulites prinus*, Flower 1964*a*, pl. 5, fig. 5; *Baruesoceras expansum*, Flower 1964*a*, pl. 9, figs 7–8; *Baruesoceras percurvatuu*, Flower 1964*a*, pl. 13, fig. 2; *Boreoceras washburni*, Flower 1964*a*, pl. 16, fig. 5; *Muriceras gracile*, Flower 1964*a*, pl. 25, fig. 25 (?); *Huyuanoceras shanxiense*, Chen and Teichert 1983, pl. 5, fig. 1; *Aracoceras eudogastricum*, Chen and Teichert, 1983, pl. 6, fig. 4 (?); *Physalactinoceras beuiense*, Chen and Teichert, 1983, pl. 5, fig. 5): differing carbonate textures adapically and adorally may represent different types of infill, and thus differing taphonomic histories for each part of the conch. However, these examples have complicated diagenetic histories and are difficult to interpret with any certainty without studying the original material.
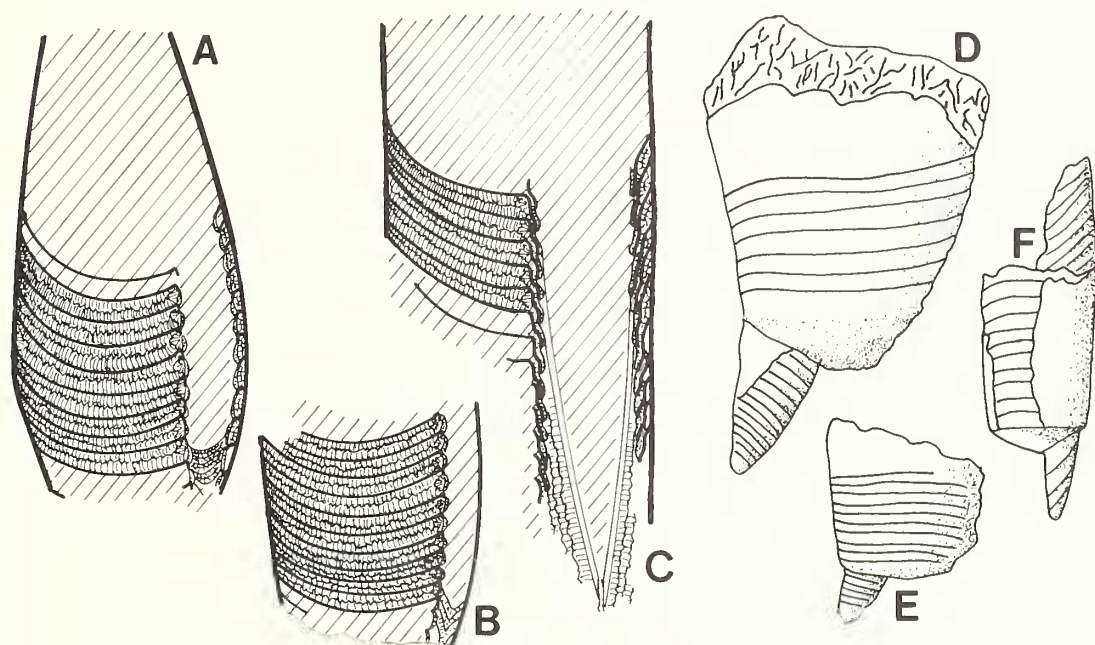
TEXT-FIG. 4. A–C, three specimens discussed in the text showing distribution of various infills; diagonal shading represents sediment infill, parallel lines broken by zigzags represent sparite in the camerae and between siphonal diaphragms where they have not been damaged before burial; A, *Pictetoceras eichwaldi* Foerste (see Mutvei and Stumbur 1971, pl. 1, fig. 1); B, Cyclostomiceratidae gen. et sp. nov.; C, *Dideroceras* sp. nov. D–F, examples of North American ellesmerocerids and endocerids which may show similar preservational features to the cephalopods recovered from Priestweston and Camnant; D, *Cassinoceras explanator* (Whitfield) (after Ulrich *et al.* 1943, pl. 7, fig. 1); E, *Caseoceras nitidum* Ulrich, Foerste and Miller (after Ulrich *et al.* 1943, pl. 41, fig. 5); F, *Pachendoceras huzzahense* (Ulrich and Foerste) (after Ulrich *et al.* 1943, pl. 61, fig. 1); all may represent phragmocones where apical truncation took place close to the most adoral development of diaphragms or endocones.

Stridsberg (1984, p. 10) noted that the apical ends of oncocerids from the Silurian of Gotland were always missing, even from specimens sectioned *in situ*. Stridsberg mentioned Raup's (1973) suggestion that shell implosion would take place during sinking if the entry of fluid was inhibited to part of the conch, resulting in a build-up of external pressure that would eventually cause failure

of the phragmocone wall and implosion of the gas-filled part of the shell. Stridsberg pointed out that the water depth was probably too shallow for this to happen. Such a phenomenon requires the blocking of the apical part of the siphuncle. It is not known whether such blockages exist in these taxa, but it seems possible that the type of damage described might be similar. It is in any case argued below that implosion during sinking is more likely to have resulted from septal failure than from failure of the phragmocone walls.

Amongst endocerids, many genera are known only from the endosiphuncle and what little remains of the ectosiphuncle. It can be argued that this form of preservation may have resulted because the endosiphuncle was the most resistant part of the phragmocone, surviving long after the rest of the shell had been destroyed. While this may be true, the observations made above and the interpretation below suggest that in some cases damage may have occurred during a specific sequence of events.

INTERPRETATION

Interpretation of preservation is similar for both forms (Text-fig. 5). Sparite infilling intact camerae adoral to the development of diaphragms or endocones may indicate that, after the death of the organism, adoral camerae were flooded without the rupture of connecting rings taking place, for there is no evidence of connecting ring damage. Whether the phragmocone sank after death, or was already lying on the substrate, the adoral camerae rapidly reached equilibrium with the ambient pressure.

Camerae adapical to the most adoral development of the diaphragms or endocones are either missing or badly damaged: this indicates that they were subjected to a traumatic event which did not affect the adoral camerae. Thus it is likely that differences in the adapical part of the phragmocone may have been a factor in causing the damage. It seems likely that the damage was the result of implosion of the adapical portion of the phragmocone.

Implosion has been given as the cause of destruction of septa in nautiloids from the Silurian of the Bohemian Basin (Westermann 1985) and in nautiloids from the Eocene London Clay Formation (Hewitt 1988). In the former, implosion was interpreted as having occurred through failure of the connecting rings followed by implosion during post-mortem sinking. Hewitt (1988) noted a variety of preservations involving imploded septa and attributed them to a range of differing post-mortem histories.

The post-mortem history of the present material is not easy to interpret, as extreme adoral parts of the conch are missing. In the few examples where body-chambers are preserved there is no evidence of damage of a type that might be attributable to predation. The similar sizes of the phragmocones and the presence of septal approximation in some individuals of the cyclo-stomiceratid suggest that they were mature (Text-fig. 3), although this may not have been the case for *Dideroceras* as there appear to be differences in the extent of development of the endosiphuncle between individuals.

Internal moulds of phragmocones from the Camnant Brook section have intact septa, septal necks and connecting rings. It is therefore unlikely that sediment penetrated into the camerae via the siphuncle. Instead, sediment must have entered through the phragmocone walls, indicating that they had been punctured through impact with the substrate or other clasts. This is consistent with the evidence for transport of fossils at Camnant Brook. Specimens from Priestweston Quarry were not subjected to such conditions and consequently are preserved with camerae containing sparite only, or as empty moulds.

It seems safe to assume that the phragmocones filled with water without the connecting rings rupturing. However, it is uncertain if the phragmocone flooded by rapid or slow filling (Crick 1983, p. 1110). Uncertainty about filling rates exists even though the connecting ring is intact and there is no evidence of cameral implosion in the adoral part of the phragmocone. The reasons are as follows.

1. The ratios of the siphonal surface areas to the cameral volumes are greater than those of *Nautilus*.
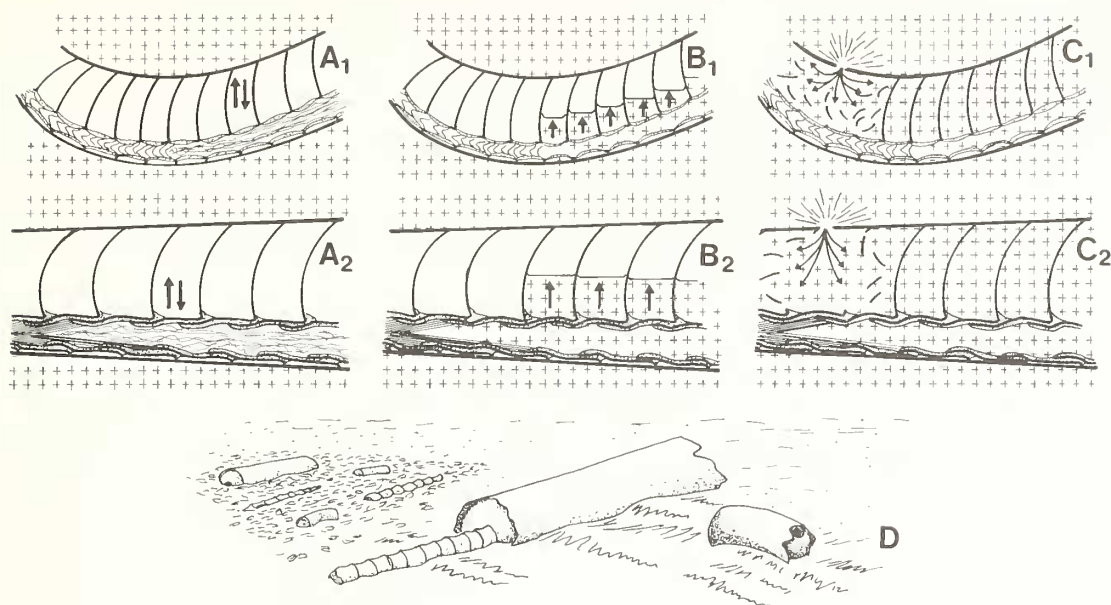
TEXT-FIG. 5. Interpretation of the history of phragmocone damage for *Dideroceras* sp. nov. (A_1–C_1) and Cyclostomiceratidae gen. et sp. nov. (A_2–C_2). A, living organism: fluid flow in and out of camerae in equilibrium and camerae empty or partly empty. B, after death: fluid flows into the phragmocone; flow into the adapical part of the phragmocone is substantially retarded or cut off by the presence of siphonal diaphragms or endocones. C, the adapical portion of the conch remains in hydrostatic disequilibrium for a substantial period; degradation of shell material and/or bending stresses and/or impacts with substrates or clasts results in implosive flooding of the vacuate part of the conch, destroying most of the adapical portion of the conch. D, undamaged portions of phragmocones and endocones buried (intact phragmocones commonly invested with sparite) as at Priestweston Quarry, or transported into storm lags with additional damage and penetration of sediment as at Camnant Brook.

2. Differences in siphuncle permeabilities when compared with *Nautilus* are uncertain.

It is considered here that the part of the phragmocone adapical of the most adoral development of diaphragms or endocones either failed to fill with liquid, or filled at a greatly reduced rate compared with the adoral portion of the siphuncle (Text-fig. 5B_{1-2}). While remaining empty or partly flooded, this part of the siphuncle would have been susceptible to implosion. Since there is no evidence that the implosion took place through the failure of the septum of the most adapical camera directly coupled to the siphuncle (since the connecting rings and septa appear to be intact), the only alternative is that the wall of the adapical part of the phragmocone failed, allowing a sudden influx of liquid which destroyed all or most of the septa and the phragmocone wall (Text-fig. 5C_{1-2}). The implosion of the adapical portion of the phragmocone occurred either while the conch was sinking through the water column or after the conch had settled on the substrate.

The nature of the damage makes it difficult to recognize which of these possibilities is correct for the present material. This is because the criterion used to recognize implosion during sinking – the preferred position of rest of septal fragments in the void created by septal implosion (Westermann 1985, p. 79) – cannot exist when the phragmocone wall has been destroyed as well. It is here argued that implosion probably took place on the substrate. Although there is little direct evidence, the main argument is that implosion must have involved the failure of the phragmocone wall and, unless bending stresses were also involved, the overall stress on the conch wall was that of a comprehensive membrane stress, with inhomogeneities probably developed at sutures and between the flooded and empty portions of the phragmocone. Because the stress was compressive,

its threshold for failure would seem likely to have been greater than that of the septa. Thus it would seem more likely that failure would have occurred through the collapse of the septum of the most adapical flooded camera. Such a process might be expected to leave the phragmocone wall intact resulting in a void containing septal fragments. Since there is no evidence of such damage to the relevant septum, and it would be expected that the apical part of the phragmocone might have been preserved in such a case, it is more likely that the adapical part of the phragmocone was lost through failure under bending stresses or through impact with other objects. As it is considered that the phragmocone wall should have been stronger than the apical-most preserved septum – and this did not fail through being over-stressed – it is more likely that the phragmocone was still intact when it reached the substrate. If the penetration of liquid into the adapical part of the conch was greatly delayed, then it seems possible that degradation of the organic portion of the shell assisted in reducing the stress threshold for the failure of the phragmocone.

Whereas siphuncles containing endocones are generally preserved, at least as fragments, and sometimes remain attached to the more adoral part of the phragmocone, the same cannot be said for siphuncles containing diaphragms. This is caused by differences between their structures. When diaphragms have been broken and fractured, the voids between them contain sediment (Text-fig. 4a–b). When unbroken, sparite is present instead. Since the destruction of the phragmocone must have occurred after the death of the organism, sediment must have invaded the voids between diaphragms at this time. This indicates that the spaces between diaphragms must have been empty or fluid-filled during life. Thus, it seems likely that the calcite commonly observed between diaphragms was precipitated after death. If so, the siphuncle essentially consists of a tube periodically partitioned by diaphragms. Compared with densely packed endocones, a siphuncle possessing diaphragms would probably be mechanically weak, and may well have been destroyed during the implosion of the phragmocone, or remained only to be broken up shortly afterwards through attrition. Thus the condition of siphuncles with endocones (either attached to the remaining intact portion of the phragmocone or as discrete fragments remaining long after the rest of the phragmocone was destroyed) resulted from a greater mechanical robustness.

FUNCTION OF SIPHONAL DIAPHRAGMS AND ENDOCONES

The interpretation above implies that siphonal diaphragms and endocones were responsible for stopping or impeding the flow of lipid into the apical camerae which then imploded, possibly through a combination of increased hydrostatic pressure and gradual deterioration of shell strength.

Diaphragms have been interpreted as extensions of the connecting ring (Flower 1964b, p. 20). Mutvei and Stumber (1971, p. 120, pl. 1, fig. 2) showed that for *Pictetoceras eichwaldi* the diaphragms formed a structure separate from the connecting ring. This may be so for all cephalopods bearing primary diaphragms. Diaphragms must be secreted later than the connecting rings with which they are associated. This is because there should be a period between the formation of the connecting ring and the removal of most of the cameral fluid. It would be expected that diaphragm secretion took place after the cameral fluid had been removed. The situation may be emphasized where crowding of diaphragms takes place, since prolonged periods between the secretion of the connecting ring and that of the diaphragms may exist. It is therefore possible to say that the connecting ring and the diaphragm are separate entities insofar as they could not have been secreted at the same time. However, were they similar in composition to the connecting rings? Clearly they were not differentiated into a number of layers as were many ellesmerocerid connecting rings.

Occurrence of sediment between damaged adapical diaphragms and calcite between undamaged adoral diaphragms is taken to indicate that the calcite was precipitated after the phragmocone imploded, and was inorganic in origin. If such is the case, then the sparite present between the diaphragms could only have been precipitated if the diaphragms themselves were porous. It seems probable that both the diaphragms and connecting rings were porous. Despite this porosity it would appear that the adapical part of the phragmocone remained empty of liquid for much of the life of the organism and for some period after its death.

The groups possessing primary diaphragms (as opposed to the secondary diaphragms seen in some endocerids, orthocerids and discosorids, which were deposited later than the main phase of endosiphonal deposits) include the Plectronoceratida, Protactinocerida, Yanhecerida and some Ellesmerocerida. Of these, many may have possessed a hydrostatic poise in which the apical part of the phragmocone was positioned above the body-chamber; most were small and in those forms which were longiconic, there is little sign of a structure which could have counterbalanced the organism, bringing it a horizontal poise. If the Cephalopoda originated from monoplacophorans similar to *Knightoconus* (Yochelson *et al.* 1973), then such a poise might be expected in early cephalopods. With such a poise, the apical camerae would have remained empty for most of the organism's life. Once emptied, they were no longer involved in hydrostatic readjustment, and a marked pressure gradient would have existed between the gas in the camerae ($9 \cdot 22 \times 10^{-1}$ N m^{-2} for *Nautilus* according to Denton and Gilpin-Brown 1966, p. 750) and the fluid in the tissues, which was at the ambient hydrostatic pressure. While it is clear from *Nautilus* that, once emptied, camerae do not normally flood, the large pressure gradient would suggest that fluid ought to leak from the siphuncle into the camerae. Since this does not happen, there must either be a physical barrier which is impermeable to such leakage or pumping is maintained at a level which exactly counteracts the leakage. There is little evidence for the existence of a physical barrier. Studies by Greenwald *et al.* (1980) and Ward and Greenwald (1982) indicated both that the siphonal pump could be switched off (in which case camerae reflooded) and that its activity could be increased by artificially flooding camerae. It is suggested here that siphonal pumping is maintained at an equilibrium level: exactly counterbalancing the tendency to flood. Maintenance of pumping therefore has a metabolic cost, both in terms of actual pumping and in maintenance of siphonal tissue.

The withdrawal of the siphuncle by resorption of tissue, followed by the precipitation of a diaphragm, may have provided a metabolic saving. Since the evidence suggests that the diaphragms were permeable, pumping may have persisted to keep the adapical camerae from flooding. However, the pumping requirement was greatly reduced.

Chamberlain and Moore (1982) discussed flow rates across the connecting ring in *Nautilus*, concluding that the degree of permeability in the material making up the connecting ring was a major contributory factor, while geometric factors (surface area to thickness ratio of the connecting ring) were less important. Despite this, it is argued that diaphragms were of importance because they greatly reduced the ratio of the siphuncle surface area to cameral volume for the adapical camerae. Thus the rate at which fluid could leak into adapical camerae would be much reduced. Secondly, the pressure head on the most adoral diaphragm would be no different from that on the connecting ring. This means that even if the permeability of the diaphragm was similar to that of the connecting ring, the rate of pumping of the siphonal epithelium at the diaphragm need be no greater per unit area than any other part of the siphuncle, but would curtail the flooding of a large volume of phragmocone at a much reduced metabolic expense. Since intraspecific variation in the permeability of connecting rings has been demonstrated in *Nautilus* (Chamberlain and Moore 1982), it may be reasonable to speculate that the conchiolin forming the diaphragms may have been less permeable than that of the connecting rings. The presence of many diaphragms, especially if closely packed, would also reduce permeability.

Crick (1988, p. 26) stated that communication was not possible between the siphuncle and the endocone-sealed camerae. Endocones are often pervasively recrystallized and the original laminae obscured. This may be taken to indicate that they were subjected to a neomorphic process at some stage of their diagenesis. However, well-preserved endocones retain a laminate structure while the interlaminae consist of sparite. The presence of the sparite may suggest that the endocones originally formed sheaths of permeable material of fabric similar to that of the connecting rings. Whether the sparite was deposited during life cannot be demonstrated, but it is likely that some homology may exist between diaphragms and endocones, since both could have acted to reduce the degree of back flow from the siphuncle into previously emptied camerae.

The endocone has been proposed as serving as a counterbalance and anti-roll device (Flower 1955, p. 94; Furnish and Glenister 1964, p. K120). Modelling of buoyancy by Westermann (1977)

may suggest that the camerae associated with the endocone-bearing portion of the siphuncle were entirely flooded. If so, the hypothesis explaining the damage described above would be invalid. Only further modelling of buoyancy and the recovery of well-preserved, relatively complete conchs will help to resolve this. Here, it is suggested that the taphonomic evidence indicates that such camerae were incompletely flooded. If so, then endocones must have been more extensively developed than in Westermann's model if they were controlling hydrostatic poise. It is probable that endocones were homologous with siphonal diaphragms and developed a secondary function in the control of hydrostatic poise.

SYSTEMATIC NOTE ON *DIDEROCERAS*

Dideroceras has been considered a junior synonym of *Protovaginoceras* (Teichert 1964, p. K157). Recent studies of type and topotype material of *Proterovaginoceras* and *Dideroceras* by Dr A. H. King (in prep.) show that the genera are distinct. *Dideroceras* differs from *Proterovaginoceras* in having shorter septal necks, and a smaller pre-septal cone. In addition there are marked differences in the form of the endocones (A. H. King, pers. comm.) These differences are sufficient to distinguish endocerids at generic level.

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